INTERNAL STRUCTURAL FEATURES OF THE SHELL OF MIDDLE CALLOVIAN AMMONITES

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ABSTRACT: The scanning electron microscope was used to study the structure of the protoconch wall, the nepionic ridge, the first and subsequent whorls, the septa, the septal necks and their accompanying elements (cuffs and annular deposits) in Middle Callovian ammonites belonging to the families Cardioceratidae (Cadoceras, Pseudocadoceras) and Kosmoceratidae (Kosmoceras, Sigaloceras). The members of the two families have been found to have features in common and differences. Information is given concerning the size of the protoconch, the caecum and the fixator, and concerning ontogenetic alteration in the height of the whorls, the diameter of the siphuncle and the number of septa.

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The preliminary results of a study of the protoconch and phragmocone in Middle Callovian members of the genera Cadoceras, Pseudocadoceras and Kosmoceras have been examined in a recently published paper (Drushchits, Doguzhayeva and Lominadze, 1976). These studies were subsequently continued; the genus Sigaloceras was additionally investigated. We were able to examine some shells with a scanning electron microscope (SEM). All the specimens investigated were collected in the main from Middle Callovian clays on the left bank of the Oka River at Yelat'ma village (Ryazan Province). Organic structures - fixator (prosiphon), caecum and siphuncle - have been preserved in many of the ammonites.

Cadoceras and Pseudocadoceras are of the family Cardioceratidae; Kosmoceras and Sigaloceras of the family Kosmoceratidae. These genera and families have long attracted attention. Their external characters have been described in some detail and the alteration of the suture line in the course of ontogeny has been investigated (Bodylevskiy, 1926; Shevyrev, 1960; Schindewolf, 1965). Nevertheless, the systematic position of the families to which these genera belong remains open to dispute. Arkell (Arkell, Kummel and Wright, 1957) places the families Cardioceratidae and Kosmoceratidae in the superfamily Stephanoceratoidea. In Principles of Paleontology (1958) they were placed in different superfamilies: the family Kosmoceratidae (along with the families Parkinsoniidae, Reineckeiidae and Morphoceratidae, which have nothing in common with the Kosmoceratidae and are now accorded to the superfamily Perisphinctoidea) in an eponymous superfamily, while Arkell's proposal was accepted for the Cardioceratidae.

Shevyrev (1960), who was convinced that the scientific classification of ammonites had to be phylogenetic, relied on ontogenetic studies and demonstrated the taxonomic importance of the suture line at different systematic levels. According to his data and to our own observations, very early inception of the second inner lateral lobe I^1 is to be observed in the ontogenetic development of members of the superfamily Stephanoceratoidea (including the family Kosmoceratidae) and the suture line is complicated by inner lateral lobes. Thus, for example, the final formula of the line is as follows in the genus Sigaloceras: (V_1V_1) $(U_2U_1U_2)$ $U^1I_1I^2I^3{:}I_1I^1D$, while in Kosmoceras the final suture line has one lobe more: (V_1V_1) $(U_2U_1U_2)$ $U^1I_1I^2I^3{:}I^4I_1I^1D$.

Like kosmoceratids, members of the family Cardioceratidae are typified by very early inception of the second inner lateral lobe I^1, but in contrast to most of the Stephanoceratoidea, it is by the umbilical lobes that the suture line is complicated in members of this family. When we investigated the suture line in the ontogeny of cardioceratids (subfamily Cadoceratinae, genera Cadoceras, Pseudocadoceras, Longaeviceras and Quenstedtoceras), we found that development of the line was completely identical until a stage corresponding to the formula: (V_1V_1) $(U_2U_1U_2)$ $U^1U^2U^3{}_1U^4U^3{}_1II^1D$. It is only in the final stages that the differences between the genera emerge.

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Complication of the suture line by the umbilical lobes is also to be seen in members of the family Macrocephalitidae (Schindewolf, 1965; Lominadze, 1967). It is on this basis that Shevyrev (1960) quite correctly combines the families Macrocephalitidae and Cardioceratidae in the superfamily Macrocephalitoidea.

Schindewolf (1965) differs in considering that neither the Macrocephalitidae nor the Cardioceratidae can be removed from the superfamily Stephanoceratoidea, and that there is no need to combine them in the new superfamily Macrocephalitoidea, as proposed by Shevyrev. According to Schindewolf, development of the suture line is monotypic in kosmoceratids, macrocephalitids and cardioceratids.

The authors undertook the present investigations in view of the differences of opinion concerning the systematic position of the genera and families under consideration, based mainly on suture line ontogeny, and also because of the lack of information on the internal structure of their shells.

The scanning electron microscope was used to investigate the microstructure of the protoconch wall, the nepionic ridge and the subsequent whorls, the septa and septal necks and their accompanying cuffs and annular deposits. Two protoconch diameters were measured in median section: the greater diameter passing through the proseptum (D^1), and the lesser diameter perpendicular to it (D^2), the diameter of the shell of the ammonitella (Dam), the diameters of the corresponding whorls (D_1, D_2 etc.), the diameter of the caecum measured along the spiral (C_1), and a second diameter measured perpendicular to the first (C_2), the length of the band of the fixator (the term is proposed as a replacement for "prosiphon", Drushchits, 1976), the number of septa to each whorl (W_1, W_2 etc.) and the distance between them, the height of the whorls of the spiral measured every half-whorl ($H_{0.5}$, H_1, $H_{1.5}$ etc.), the diameter of the siphuncle from the point at which the caecum gives way to the siphuncle (S_0) and after every 180° ($S_{0.5}$, S_1, $S_{1.5}$ etc.), the ratio of siphuncle diameter to whorl height (S_0/H_0, S_1/H_1 etc.), the ratio of the height of each successive whorl to the preceding one (H_1/H_0, $H_{1.5}/H_{0.5}$ etc.) calculated at intervals of half a whorl (180°) for the corresponding heights. The angle of the nepionic line was determined as the angle between two straight lines constructed from the center of the protoconch to the proseptum and from the center to the nepionic line located in front of the nepionic ridge. (The nepionic line at the end of the nepionic ridge on the shell defines the position of the apertural margin of the ammonitella. A line that arose from the nepionic ridge on the cast was previously mistaken by us for the nepionic line.)

Ammonitella (Drushchits and Khiami, 1970) is the name applied to the first or juvenile (Ivanov, 1971, 1975) stage in the postembryonic development period of ammonites. It had a shell consisting of the protoconch, the first whorl as far as the nepionic line and, probably, one or two septa. This stage lasted throughout the planktonic mode of life of the juvenile ammonite, i. e. from the time of hatching from the egg to the end of the formation of the nepionic ridge. After its construction had been completed and the ammonite had transferred to the mode of life peculiar to the species (nektonic, nektonic-benthonic or benthonic) a new period began, the adolescent period, during which the shell wall that was constructed differed in structure from the single prismatic layer in the wall of the protoconch and the first whorl, and there was formation of new septa of lamellar microstructure and a new type of shell in heteromorphous ammonites (Drushchits, Doguzhayeva and Mikhaylova, 1977).

Only previously unknown structural characteristics of the shell are described below.

Family CARDIOCERATIDAE H. Douvillé, 1890

Subfamily CADOCERATINAE Hyatt, 1900

Cadoceras Fischer, 1881

Material. C. tschefkini Orb. - six spec., C. modiolare Orb. - one spec., Cadoceras sp. - one spec.

In median section the protoconch is ellipsoidal with a slightly flattened venter (fig. 1, c). In C. tschefkini the greater diameter is 0.48-0.53 (on average 0.51), the lesser diameter 0.38-0.39 (on average 0.38); the difference between the two diameters is 0.10-0.15 (on average 0.12); in Cadoceras sp. the greater diameter is 0.52, the lesser diameter 0.35; the figures for C. modiolare are respectively 0.52 and 0.38.[1] In all specimens measured the diameter of the ammonitella ranged between 0.83 and 0.88 (on average 0.86). The diameter of the first whorl was approximately one (between 1.00 and 1.16), that of the second approximately two (1.87-2.10), of the third approximately four (3.43-4.12) and of the fourth approximately eight (7.60-8.05).

[1]All linear dimensions are given in mm.

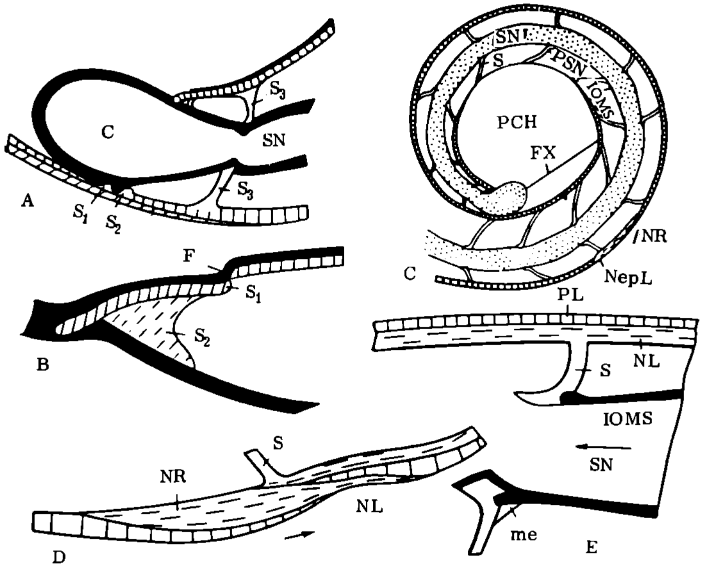

FIGURE 1. Diagrammatic sections through the shell in the genus Cadoceras:

a - caecum and commencement of siphuncle, b - junction between prosepta and protoconch wall, c - median section through protoconch and 1st whorl, d - nepionic ridge and nepionic line, e - structure of septal neck in 2nd whorl; all drawings, except 1c, made from SEM photographs.

IOMS - inner organic membrane of siphuncle, F - flange, me - membrane, PCH - initial chamber (protoconch), NR - nepionic ridge, NL - nacreous layer, NepL - nepionic line, PL - prismatic layer, PSN - prochoanitic septal neck, S, S_1, S_2, . . . - speta, SN - siphuncle, FX - fixator, C - caecum.

The wall of the protoconch and the first whorl is of prismatic microstructure. One specimen was examined by SEM. Two prismatic microlayers are distinguishable in the adoral part of the protoconch wall. One microlayer dies out around the proseptum, while the other becomes thicker (pl. II, illus. 1d, e; fig. 1, a); the first whorl is constructed from it. The nepionic line lies at a distance of 260-290° from the proseptum, in front of the nepionic ridge. The angle of the nepionic line was 260° in one specimen, 270° in the other. The ridge is lenticular, 0.21 long and 0.04 thick (pl. II, illus. 1h; fig. 1, d). The outer part of the nepionic ridge is constructed from the gradually tapering prismatic layer, beneath which there is a nacreous layer that is thickest approximately in the middle of the ridge. Beyond the nepionic ridge the shell wall consists of two layers - an outer prismatic layer and a nacreous layer (pl. II, illus. 1f). The outer prismatic layer commences from the inside of the anterior part of the ridge and beyond the ridge it forms the outer layer of the wall of the whorl (fig. 1, d). Beneath it there is a nacreous layer forming the second (inner) layer of the wall in the final quarter of the first whorl and the whole of the second whorl. At the end of the second or the beginning of the third whorl (we were unable to establish this precisely) a third layer arises, the inner prismatic layer, and the wall of all subsequent whorls is three-layered. The thickness ratio of these layers is initially 1:1:1, but subsequently the nacreous layer gradually becomes thicker, so that by the end of the third whorl it is more than three times the thickness of each of the prismatic layers (their ratio is 1:3.25:1). The inside of the shell wall is lined in all forms with a fine conchiolin membrane. The dorsal wall is well traceable in the fourth and fifth whorls; it is 1/2 - 1/3 the thickness of the ventral wall, which it overlaps.

Whorl height changes as follows (reckoning from the beginning of the spiral and giving figures at intervals of half a whorl): H_0 = 0.11-0.14, $H_{0.5}$ = 0.22-0.24, H_1 = 0.28-0.35, $H_{1.5}$ = 0.36-0.42, H_2 = 0.45-0.53, $H_{2.5}$ = 0.70-0.83, H_3 = 1.00-1.20. The height ratio of two adjacent whorls at intervals of half a whorl alters as follows: H_1/H_0 = 2.23-2.55, $H_{1.5}/H_{0.5}$ = 1.5-2.04; H_2/H_1 = 1.6-1.83, $H_{2.5}/H_{1.5}$ = 1.49-1.97, H_3/H_2 = 1.9-2.27.

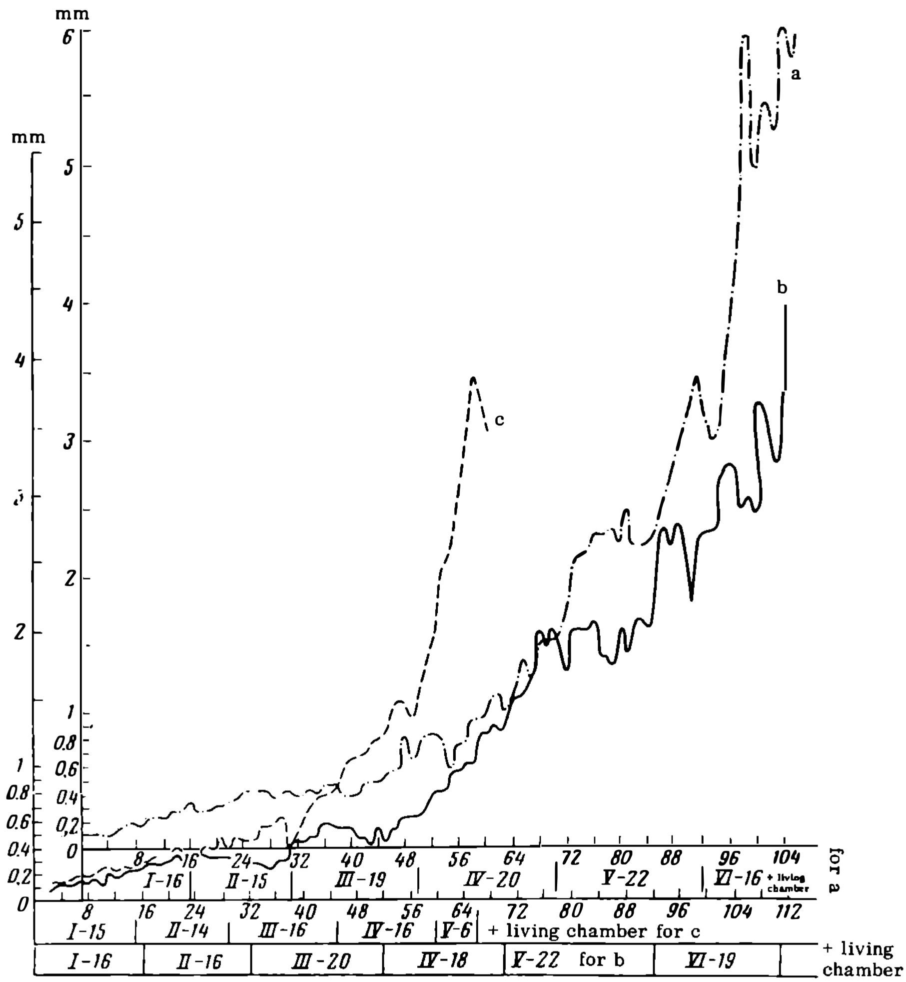

FIGURE 2. Curves depicting distances between septa in Cadoceras tschefkini and Pseudocadoceras cuneatum; a, b - C. tschefkini: a - spec. 1139, b - spec. 1137; c - Ps. cuneatum: spec. 1144; Yelat'ma village; Middle Callovian.

The fixator was preserved in five specimens; its length ranged between 0. 07 and 0. 13. It took the form of a band extending from the caecum and attached in an arc on the inside of the protoconch. Its length will therefore be least in median section and greatest in marginal section.

The caecum is of rounded or oval section extended along the spiral in eight specimens. Its greater diameter (C_1) is greater than the lesser diameter (C_2) by 0. 01-0. 04; in one case $C_2 > C_1$. In three specimens the section is rounded with equal diameters ($C_1 = C_2$). The caecum has a thick organic membrane.

The siphuncle occupies a central position in the first whorl (fig. 1, c), after which it is subcentral and becomes ventromarginal from the middle or end of the second whorl. The diameter

KEY TO PLATE I

Pseudocadoceras sp.:

1 - Spec. 189/1148 (x 1500): a) nepionic ridge, b) structure of septum in third whorl;
2 - Spec. 189/1146: a) shell wall in middle of second whorl (x 1500), b) at start of second whorl (x 3000);
3 - Spec. 189/1145, shell wall after primary ridge (x 2500);
4 - Spec. 189/1147: a) shell wall and ventral part of prochoanitic septal neck in third whorl (x 700), b) shell wall in fourth whorl (x 1400); Yelat'ma village; Middle Callovian.

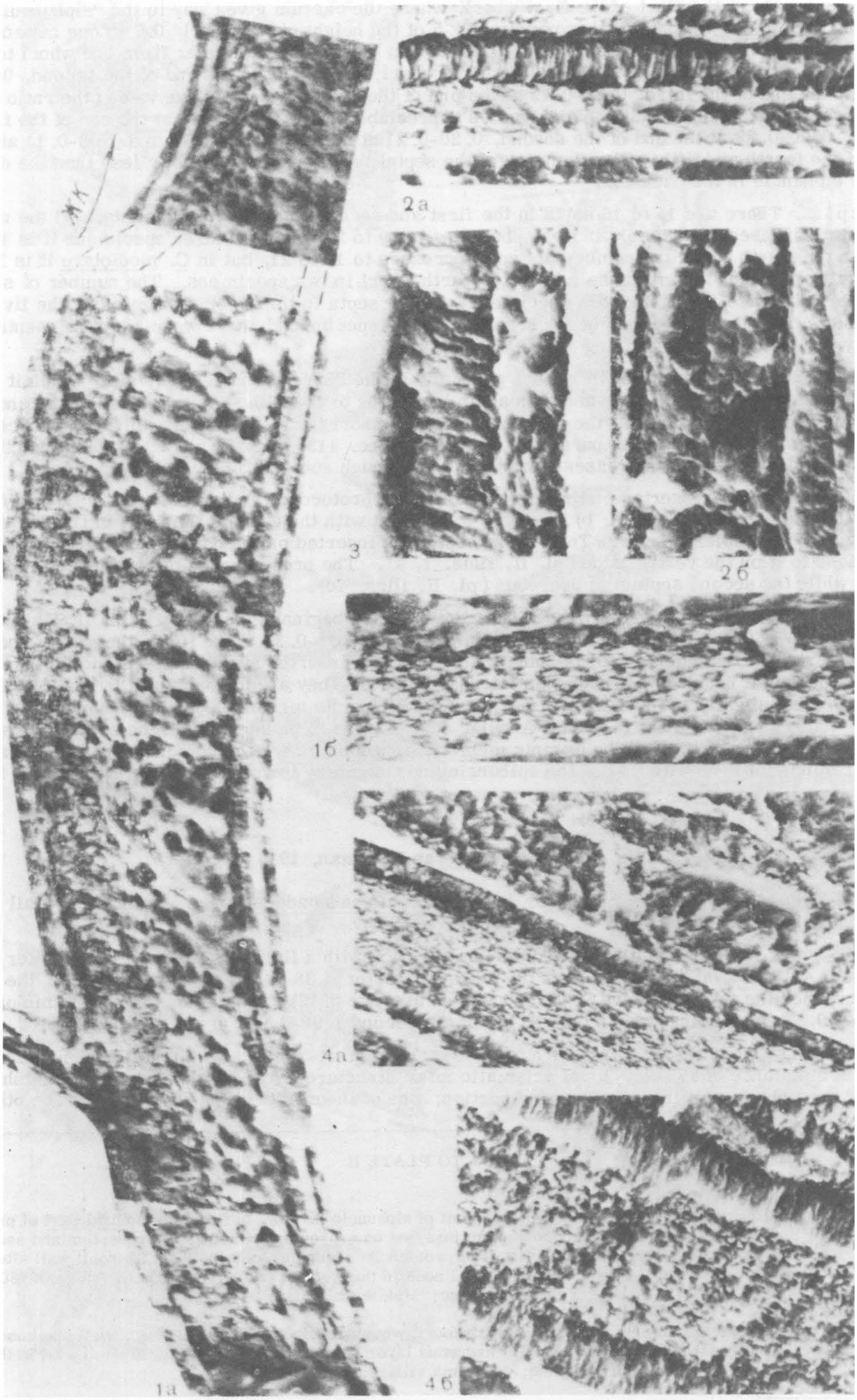

PLATE I

of the siphuncle at the start of the first whorl, where the caecum gives way to the "siphuncular strand" (sifonal'nyy tyazh) is approximately 0.5 of the height of the whorl, 0.7 in one instance. Thereafter, although there is an absolute increase in siphuncular diameter from one whorl to the next (it is on average 0.1 at the end of the first whorl, 0.13-0.14 at the end of the second, 0.20-0.27 at the end of the third, 0.32-0.45 at the end of the fourth), its relative value (the ratio of siphuncular diameter to whorl height) varies appreciably. It is 0.25-0.38 at the end of the first whorl, 0.20-0.29 at the end of the second, 0.20-0.21 at the end of the third and 0.08-0.11 at the end of the fourth and fifth. The diameter of the septal neck is usually slightly less than the diameter of the siphuncle in the chamber.

Septa. There are 15 to 16 septa in the first and second whorls; in the third whorl the number of septa increases appreciably in five specimens to 19 to 20, while in three specimens it is 14 to 15. In the fourth whorl the number of septa increases to 19 to 21, but in C. modiolare it is 14. The living chamber begins at the end of the fourth whorl in two specimens. The number of septa reaches 22 in the fifth whorl; one specimen has eight septa in this whorl, followed by the living chamber. The sixth whorl had been preserved in two specimens; there were 16 and 19 septa respectively, followed by the living chamber.

The distance between septa increases gradually to the 38th to 42nd septum, after which it decreases slightly (septa 35, 40) and then again increases to the 48th septum located at the end of the third whorl (fig. 2, a, b). At the start of the fourth whorl the distance between septa reduces abruptly, as is expressed with particular clarity in spec. 1139 (fig. 2, a). Beginning with the fourth whorl the distance increases continuously, although subject to marked fluctuations.

The proseptum is inserted on the dorsal wall of the protoconch at its very end, without a flange (pl. II, illus. 1 a-c; fig. 1, a, b). Before its contact with the caecum this part of the proseptum is long and resembles a lever. The second septum is inserted on the dorsal part of the proseptum and close to it on the ventral side (pl. II, illus. 1, a). The proseptum is of prismatic microstructure, while the second septum is nacreous (pl. II, illus. 1c).

The septal necks are prochoanitic from the very beginning, and short (pl. II, illus. 1g). Their length is 0.07-0.10 in the third to fourth whorls, 0.31-0.35 in the fifth; the part of the septal neck inserted on the ventral wall is shorter than the part inserted on the opposite side. Like the septa, the septal necks are of nacreous microstructure. They are accompanied by short cuffs, which project slightly to the rear and merge with the organic membrane of the siphuncle, which enters the septal neck from in front. Annular deposits are to be seen within the septal necks as a small patch above the cuff. The organic membrane, which covers the septum from in front and from behind, joins up with that of the spihuncle and frequently forms an organic membrane (fig. 1, e).

Pseudocadoceras Buckman, 1918

Material. Ps. cuneatum Sasonov 1 one spec., Pseudocadoceras sp. - four spec.; all examined with a SEM.

The protoconch is ellipsoidal in median section with a flattened venter. The greater diameter is 0.49-0.55 (on average 0.51), the lesser diameter 0.38-0.40 (on average 0.38); the difference between the two diameters is 0.11-0.15 (on average 0.12). The diameter of the ammonitella is 0.83-0.87, of the first whorl 1.05-1.15, of the second 1.86-2.07, of the third 3.57-4.07.

The wall of the protoconch and of the first whorl as far as the nepionic ridge lying at a distance of 270-280° is of prismatic microstructure. Three layers are distinguishable in the protoconch wall in one preserved portion; one of them is twice the thickness of the others.

KEY TO PLATE II

Cadoceras sp.:

1 - Spec. 189/1131: a) caecum and commencement of siphuncle (x 400), b) flange and mural part of proseptum, detail of 1c (x 3000), c) second septum inserted on proseptum (x 2000), d) proseptum and second septum from ventral side (x 2000), e) wall of protoconch around caecum (x 2000), f) shell wall after nepionic ridge (x 1000), g) prochoanitic septal neck in third whorl (x 400), h) nepionic ridge (x 280); Yelat'ma village; Middle Callovian.

Kosmoceras sp.:

2 - Spec. 189/1105; a) outer part of shellwall in fourth whorl, moving downwards: dorsal wall and conchiolin layer, outer prismatic layer and part of nacreous layer of ventral wall (x 2500), b) shell wall in third whorl (x 1500); Yelat'ma village; Middle Callovian.

Pseudocadoceras sp.:

3 - Spec. 189/1146, prochoanitic septal neck, cuffs and annular deposits in fifth whorl (x 650); Yelat'ma village; Middle Callovian.

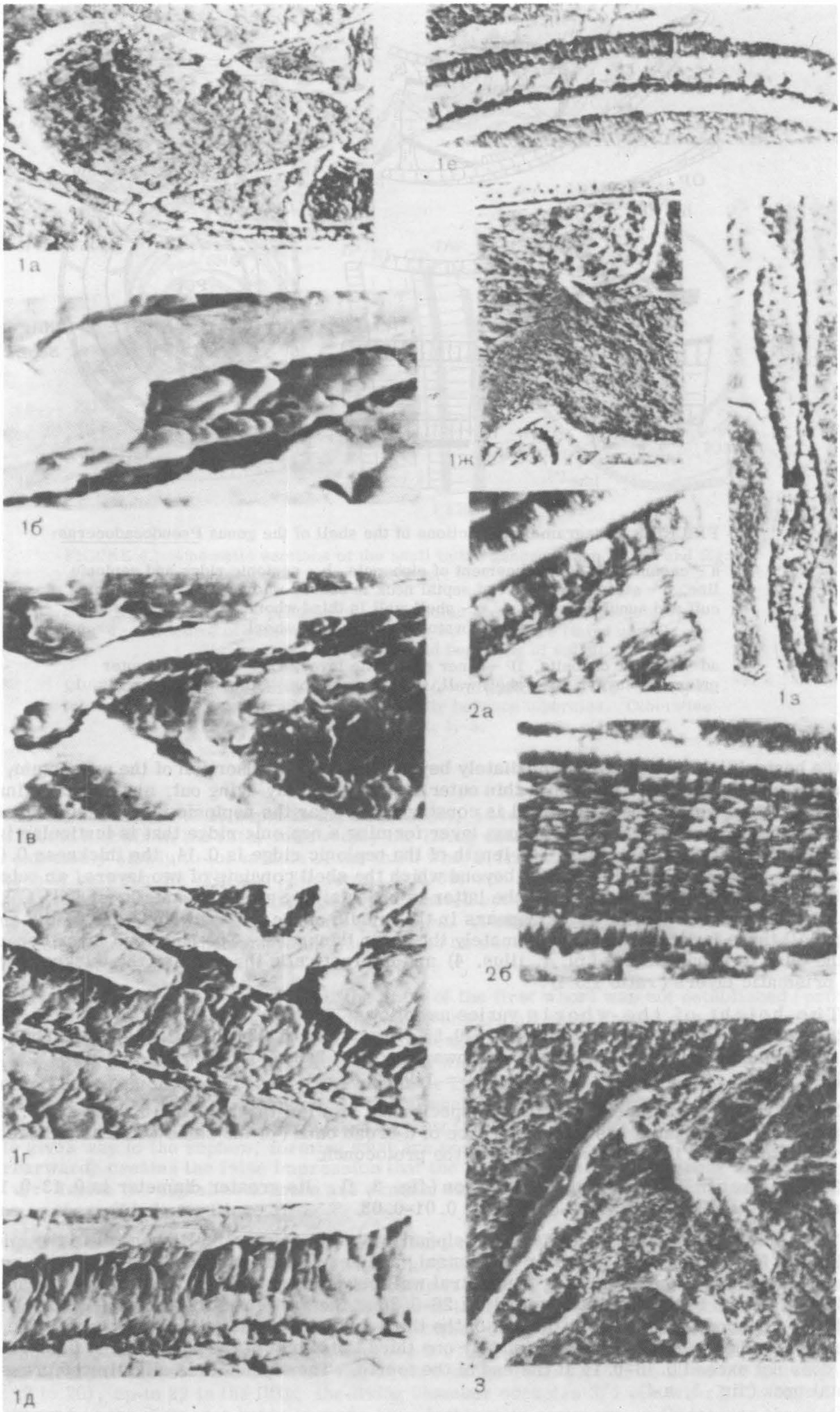

PLATE II

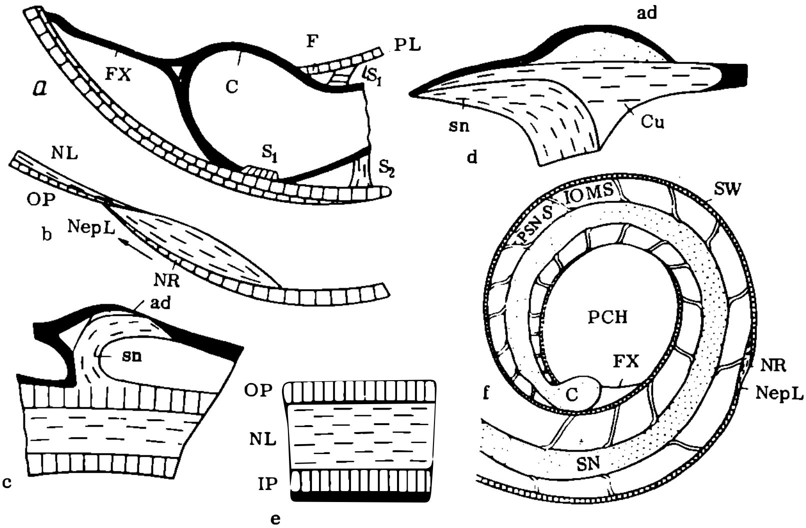

FIGURE 3. Diagrammatic sections of the shell of the genus Pseudocadoceras:

a - caecum and commencement of siphuncle, b - nepionic ridge and nepionic line, c - structure of part of septal neck in second whorl, d - septal neck, cuff and annular deposits, e - shell wall in third whorl, f - median section through protoconch and first whorl.

ad - annular deposits, IP - inner prismatic layer, Cu - cuff, OP - outer prismatic layer, SW - shell wall, sn - septal neck. Otherwise as on Fig. 1.

At the beginning of the spiral, immediately beyond the point of insertion of the proseptum, the wall consists of two prismatic layers: a thin outer layer, gradually dying out, and a thicker inner layer, from which the wall of the first whorl is constructed. Near the nepionic ridge this prismatic layer peters out; above it there is a nacreous layer forming a nepionic ridge that is lenticular in longitudinal section (pl. I, illus. 1a). The length of the nepionic ridge is 0. 14, the thickness 0. 03. In front of it there is the nepionic line, beyond which the sheil consists of two layers, an outer prismatic and an inner nacreous layer; the latter is underlain by a thin organic layer (pl. I, illus. 2a, 2b, 3). An inner prismatic layer appears in the middle of the second whorl, and by the end of the whorl all three layers are of approximately the same thickness. The nacreous layer becomes thicker in the third to fourth whorls (pl. I, illus. 4) and is practically three times the thickness of each of the prismatic layers (ratio 1:3:1).

The height of the whorls varies as follows: $H_0 = 0.11$-0.13, $H_{0.5} = 0.22$-0.26, $H_1 = 0.28$-0.31, $H_{1.5} = 0.35$-0.42, $H_2 = 0.45$-0.55, $H_{2.5} = 0.7$-0.83, $H_3 = 1.04$-1.18. The height ratio of two adjacent whorls varies as follows: $H_1/H_0 = 2.3$-2.64, $H_{1.5}/H_{0.5} = 1.46$-1.91, $H_2/H_1 = 1.45$-1.93, $H_{2.5}/H_{1.5}$ /$= 1.92$-2.14, $H_3/H_2 = 1.95$-2.62.

The fixator was preserved in four specimens. Its length was 0. 07 in some and 0. 13 in others (fig. 3, a). The fixator has the appearance of a broad band (of the same width as the caecum) inserted in an arc on the concave surface of the protoconch.

The caecum is slightly oval in section (fig. 3, f). Its greater diameter is 0. 13-0. 14, its lesser diameter 0. 11-0. 13, the difference 0. 01-0. 03.

The caecum gives way gradually to the siphuncle, which is practically central to the middle or end of the first whorl and thereafter subcentral, and ventromarginal from the end of the second to middle of the third whorl, hugging the ventral wall between septa. The diameter of the siphuncle is 0. 31-0. 63 at the beginning of the spiral, 0. 26-0. 36 at the end of the first whorl, 0. 20-0. 29 at the end of the second, 0. 17-0. 26 at the end of the third and 0. 14 at the end of the fourth. The relative diameter of the siphuncle is approximately one third the height of the whorl in the first three whorls, but does not exceed 0. 13-0. 14 at the end of the fourth. The siphuncle is slightly compressed in the septal neck (fig. 3, a-f).

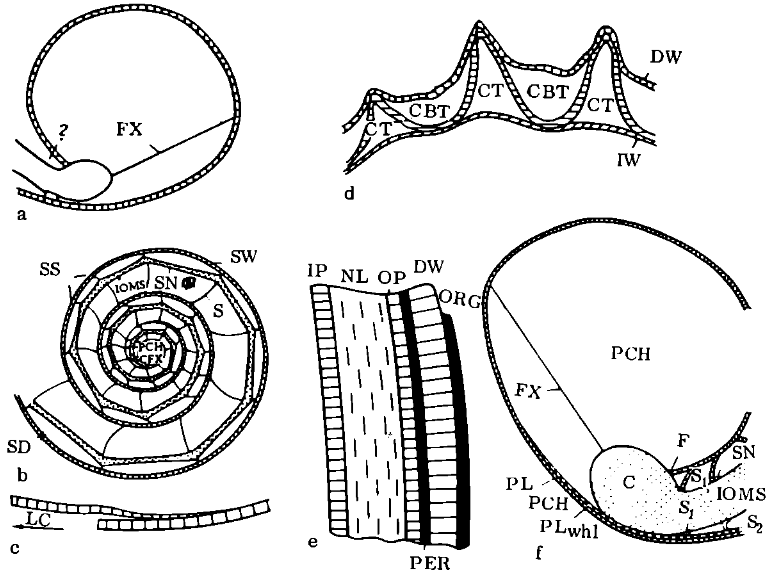

FIGURE 4. Schematic sections of the shell in the genera Kosmoceras and Sigaloceras:

a-e - Kosmoceras: a - protoconch, b - median section, c - damage during life, d - structure of ventral tubercles, e - wall structure (third whorl); f - Sigaloceras, protoconch and beginning of spiral.

DW - dorsal wall, SD - site of damage, ORG - organic layer, CT - cavity of tubercle, PER - periostracum, CBT - cavity between tubercles. Otherwise as on Figs. 1, 3.

Septa. There are 15 to 17 septa in the first whorl, 14 to 16 in the second, 16 to 17 in the third, 15 in the fourth and six in the fifth, followed by the living chamber. The distance between septa increases extremely slowly to the middle of the third whorl (from 0.08 to 0.63), after which it reduces abruptly between the 37th and 38th septa (to 0.39) and subsequently increases comparatively rapidly. A slight reduction in the distance is to be noted between the 55th and 56th septa, after which the distance between septa once again increases. A characteristic final reduction in the distance between the ultimate and penultimate septa is to be seen (fig. 2, c). The microstructure of the septa is lamellar (pl. I, illus. 1b).

The direction of the septal necks at the start of the first whorl was not established (probably prochoanitic). From the middle of the second whorl onward all septal necks are prochoanitic and short. Their length in the third whorl is 0.1 of the length of the siphuncle in the chamber, while in the fourth whorl it is 0.05-0.08. The cuff is located within the septal neck, frequently projecting rearward. The conchiolin membrane of the siphuncle is inserted at the rear on the cuff and extends into the septal neck. The anterior end of the septal neck gives way to the conchiolin membrane of the siphuncle, which forms an organic connecting ring (fig. 3, c). The organic membrane of the siphuncle gives way to the septum, forming what are known as organic membranes. The cuff, projecting rearward, creates the false impression that the structure of the septal neck is amphichoanitic (fig. 3, d). Inside the septal neck there are annular deposits apparently also with nacreous microstructure on the cuff (pl. II, illus. 3).

Summarizing the information obtained for members of two genera of the subfamily Cadoceratinae (Cadoceras and Pseudocadoceras), we may note the following: 1) the greater diameter of the protoconch ranges from 0.48 to 0.55, the lesser diameter from 0.38 to 0.40; 2) the diameter of the shell of the ammonitella is 0.83-0.87; 3) the angle of the nepionic line ranges from 260 to 290°, on average 277°; 4) the caecum is of ellipsoidal section (C_1 = 0.10-0.14, C_2 = 0.10-0.13); 5) the length of the band of the fixator ranges between 0.07 and 0.13; 6) there are 14 to 16 septa to each of the first two lobes, 14 to 20 in the third (on average 16 to 17), 15 to 20 in the fourth (on average 18 to 20), up to 22 in the fifth; the living chamber occupies 3/4 of a whorl; 7) curves depicting changes in the distances between septa have features in common; in Cadoceras the distance increases gradually to the fourth whorl, but rapidly after the fourth; in Pseudocadoceras a sharp increase is to be observed at the start of the third whorl; 8) the diameter of the first whorl ranges between 1. 05 and 1. 16, that of the second whorl between 1. 86 and 2. 10, of the third between 3. 65 and 4. 12; 9) the height of the whorl is 0. 11-0. 14 at the start of the spiral, doubling within 180° (0. 22-0. 26) ; the height ratio of the end of the first whorl to its beginning is 2. 3-2. 6 (on average approximately 2. 5) ; 10) the relative siphuncular diameter is approximately 0. 5 around the proseptum, approximately 0. 3 at the end of the first whorl, 0. 2 at the end of the third and 0. 1 of the height of the whorl at the end of the fourth; 11) the position of the siphuncle and its relative size vary uniformly; the septal necks are short and there are cuffs and annular deposits; the variation in the microstructure of the wall of the protoconch, the first whorl, the nepionic ridge and the remaining whorls is monotypic in the two genera.

Family KOSMOCERATIDAE Haug, 1887

Subfamily KOSMOCERATINAE Haug, 1887

Kosmoceras Waagen, 1869

Material. K. jason (Reinecke) - four spec., Kosmoceras sp. - five spec.

In median section the protoconch is practically rounded or oval (fig. 4, a). The greater diameter is 0. 39-0. 49, the lesser diameter 0. 34-0. 40; the difference between them ranges from 0. 03 to 0. 10. The diameter of the shell of the ammonitella is 0. 76-0. 85, of the first whorl 0. 86-1. 00, of the second 1. 60-1. 90, of the third 2. 86-3. 88, of the fourth 5. 10-7. 25.

The wall of the protoconch and the first whorl investigated by SEM in two specimens was constructed of a single layer with prismatic microstructure. The wall was lined externally and internally by an organic layer absent from the point of insertion of the septum. The nepionic ridge is lenticular. Its length is 0. 15-0. 17, its maximum thickness 0. 03. As is usual, the inception of the ridge is connected with a thickening of the shell wall due to the nacreous layer and gradual petering out of the embryonic prismatic layer. In front of the ridge lies the nepionic line, from the proseptum for a distance of 310-315° (between the eighth and ninth septa). After it the shell wall is made up of an outer prismatic layer and an inner nacreous layer of approximately equal thickness. In the middle of the second whorl the nacreous layer thickens. In the third whorl the shell wall consists of three layers: outer prismatic, nacreous and inner prismatic (pl. II, illus. 2a, 2b; fig. 4, e). At the end of the third whorl and in the fourth the nacreous layer is more than seven times the thickness of each of the prismatic layers.

Two instances of damage to the shell wall that were healed during life are to be seen on one specimen (fig. 4, c). The first damage is in the middle of the third whorl around the 27th septum. When this damage healed the new layer of the shell wall was created from within, at some distance from the fractured edge. During the healing of the apertural margin two septa (17th, 18th) lying at a distance of 200° were constructed closer together than the adjacent septa. The second damage to the shell wall was separated from the first by a distance of approximately 225° along the arc, between the 29th and 30th septa (first and second septa of fourth whorl). Like the first damage, the second had healed. Two septa located at a distance of 270° along the arc were closer together than the adjacent septa (fig. 4, b). It may therefore be concluded that the living chamber occupied more than 3/4 of a whorl. Similar shell damage was also found in spec. 1103 at the end of the fourth whorl. An arcuate swelling was found in the third specimen (1104) at the start of the fourth whorl in the ventral wall. The base length of the arc was 0. 42, the height 0. 11; wall thickness before the arc was 0. 06, the arc and the shell wall beyond it were half the thickness (0. 03). At 270° from this damage, in the third whorl, the distance between two septa, the 28th and 29th, was half that between adjacent septa. In this case also, the damage apparently arose around the apertural margin. The mollusk subsequently constructed the shell and attached the septum to the arcuate swelling on the inside. In a specimen investigated by us the shell consisted of 6. 5 whorls, with 13 septa in the final whorl. Its apertural margin had ears. The last six septa were converged, especially the last two.

The shell of the genus described is known to have large ventral tubercles, which are hollow and constructed of two layers; an inner prismatic layer lines the base of the tubercle, separating its cavity from the living chamber. The dorsal wall of the following whorl forms a slightly sagging bridge between two tubercles; this bridge rests on the apices of the tubercles and does not follow their inflections (fig. 4, d).

Whorl height varies in the following manner: $H_0 = 0.10\text{-}0.13$, $H_{0.5} = 0.19\text{-}0.26$, $H_1 = 0.27\text{-}0.30$, $H_{1.5} = 0.34\text{-}0.40$, $H_2 = 0.43\text{-}0.52$, $H_{2.5} = 0.57\text{-}0.75$, $H_3 = 0.74\text{-}1.03$. The height ratio of two adjacent whorls is as follows: $H_1/H_0 = 2.55\text{-}3.0$, $H_{1.5}/H_{0.5} = 1.42\text{-}1.82$, $H_2/H_1 = 1.54\text{-}1.93$, $H_{2.5}/H_{1.5} = 1.63\text{-}1.94$, $H_3/H_2 = 1.51\text{-}2.05$.

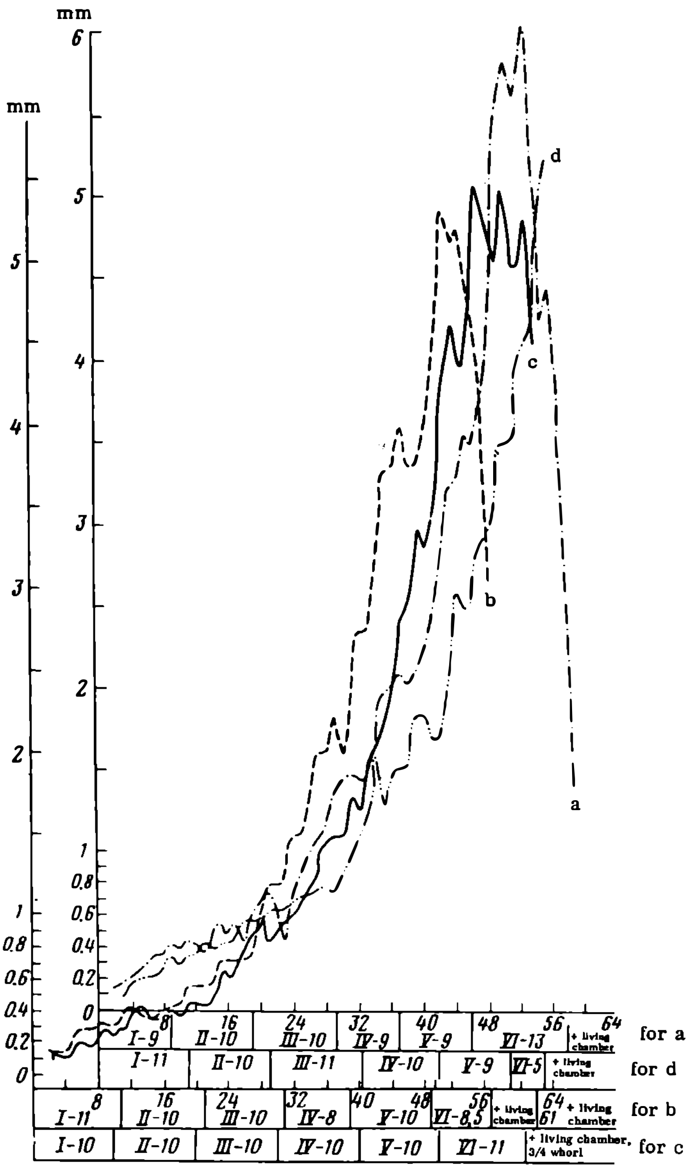

FIGURE 5. Curves showing distances between septa in Kosmoceras jason and Sigaloceras enodatum;

a-c - K. jason: a) spec. 1142, b) spec. 1140, c) spec. 1141; d - S. enodatum, spec. 1110; Yelat'ma village; Middle Callovian.

The fixator had been preserved in four specimens. Its length varied between 0.11 and 0.24 (fig. 4, a).

The caecum is slightly oval in section ($C_1 = 0.11$-0.14, $C_2 = 0.08$-0.10; C_1-$C_2 = 0.01$-0.05). It narrows at the first septum and gives way to the siphuncle.

The siphuncle occupies a central position in the first whorl, a subcentral position in the second and a ventromarginal position in the third. Because the number of septa is small (nine to eleven) and the distance between them comparatively large at the beginning of the spiral in each whorl, the siphuncle is located along a chord rather than, as in most ammonites, along an arc (fig. 4, b). Only from the end of the fourth whorl is it appressed to the ventral wall. The relative diameter of the siphuncle is 0. 20-0. 33 in the first half of the first whorl (ratio of siphuncular diameter to whorl height), 0. 21-0. 24 at the end of the second and third whorls (0. 08 in only one instance), but 0. 15-0. 21 at the end of the fourth whorl and 0. 05-0. 12 in the middle of the sixth.

Septa. There are nine to twelve septa in each of the first two whorls, predominantly ten in the third (13 in only one specimen), eight to ten in the fourth (12 in one) and nine to eleven in the fifth; in two specimens the living chamber is located after the sixth or ninth septum, in three it begins in the sixth whorl after the eighth, fifth, eleventh or thirteenth septum. The final convergence of the last two-three septa is to be seen near the living chamber (fig. 5, a-c). A very thin half of the final septum located close to the preceding septum has been preserved in one specimen. The distance between septa increases very rapidly, as is evident from the sharply rising curve. Convergence of the septa (fig. 5, a) due to damage to the shell during life in the region of the aperture existing at that time is located at a distance of approximately 270°, where there is a related slowed extension of the body for the construction of new septa. Septal microstructure is nacreous.

The septal necks are prochoanitic. They are very short in all whorls, but their absolute length increases gradually from the first whorl onward: it is 0. 10 in the third whorl, 0. 14 in the fourth, 0. 43 in the firth whorl at the penultimate septum around the ventral wall, 0. 32 on the inside. The cuffs are also short. They are located partly within the septal neck, partly projecting rearward. Annular deposits are represented by small calcareous formations within the septal necks. The connection between the siphuncular membrane and the septal necks is similar to that to be seen and described in the two preceding genera.

Summing up the information obtained for the genus Kosmoceras (subfamily Kosmoceratinae), we may note the following features: 1) the greater diameter of the protoconch ranges from 0. 39 to 0. 49, the lesser diameter from 0. 34 to 0. 39; 2) the shell diameter of the ammonitella is 0. 76 to 0. 85; 3) the angle of the nepionic line is relatively constant at 315°; 4) the caecum has a section varying from practically round to ellipsoidal (C_1 = 0. 10-0. 14, C_2 = 0. 08-0. 10); 5) the length of the band of the fixator is variable, ranging between 0. 14 and 0. 24; 6) there are ten to twelve septa in each of the first five whorls; the living chamber occupies more than three quarters of the whorl (approximately 315°); 7) the increase in the distance between septa is relatively rapid and increases with particular rapidity in the third whorl; 8) the diameter of the first whorl is 0. 86 to 1. 00, that of the second whorl 1. 70 to 1. 90, of the third 3. 00 to 3. 88; 9) the height of the whorl around the proseptum is 0. 10 to 0. 11, practically doubling through 180° (0. 20 to 0. 26); the height ratio at the end of the first whorl and at the beginning is three; 10) the relative diameter of the siphuncle is 0. 25 at the end of the first whorl, 0. 12 to 0. 22 at the end of the third and 0. 10 to 0. 20 at the end of the fourth.

Subfamily KEPPLERITINAE Tintant, 1963

Sigaloceras Hyatt, 1900

Material. S. enodatum (Nikitin) - two spec. Measurements were made on one specimen; the second was obliquely sectioned.

The protoconch is ovoid in median section, with a slightly flattened venter (fig. 4, f). The greater diameter is 0. 46, the lesser 0. 41; the difference between them 0. 05. Shell diameter is 0. 85 for the ammonitella, 0. 96 for the first whorl, 1. 85 for the second, 3. 35 for the third, 5. 9 for the fourth and 11. 0 for the fifth. The nepionic line is located at a distance of 315°. The nepionic ridge is 0. 17 long, 0. 03 thick.

Whorl height varies as follows (reckoning from the beginning of the spiral and giving figures at intervals of 180°): 0. 11, 0. 21, 0. 28, 0. 36, 0. 48, 0. 62, 0. 80, 1. 06, 1. 47, 1. 98, 2. 70, 4. 5. The height ratio of the whorls set out in order varies as follows at intervals of 180°: 2. 55, 1. 71, 1. 71, 1. 72, 1. 67, 1. 71, 1. 84, 1. 87, 1. 84, 2. 27.

The fixator was observed in one specimen. Its length was 0. 27 (fig. 4, f).

The caecum is oval in section (C_1 = 0. 10, C_2 = 0. 08, its greater diameter exceeds its lesser diameter by 0. 02). It gives way to the siphuncle around the first septum.

The siphuncle occupies practically a central position in the first whorl, a subcentral position in the second and a ventromarginal position in the third, but hugs the ventral wall approximately from the middle of the third whorl. The relative diameter of the siphuncle is 0. 55 at the start of the spiral, 0. 25 at the end of the first whorl, 0. 20 as far as the fourth whorl and 0. 10 to 0. 15 in the fifth.

Septa. There are ten to eleven septa in the first whorl, ten in the second, ten to twelve in the third, ten to eleven in the fourth and nine in the fifth; one specimen has five septa in the sixth whorl, followed by the living chamber. The increase in distance initially proceeds comparatively gradually, the distance reduces between the 32nd and 33rd septa (middle of fourth whorl), and subsequently increases rapidly once again. Two instances of shell damage that healed during life are to be seen in the second specimen (1109) at the start of the fourth whorl (around septum 35) and at the start of the fifth whorl (between the 41st and 42nd septa); convergence of two septa is to be noted at a distance of 280° from them toward the protoconch. The newly constructed part of the shell was inserted on the inside at some distance from the fractured margin; after a comparatively sharp inflection it followed a curve typical for the position of the ventral wall. The nature of the damage is similar to comparable shell damage in the genus Kosmoceras.

The septal necks are prochoanitic and short: their length is 0.14 in the fourth whorl, 0.22 in the fifth, 1/10 - 1/15 the length of the siphuncle in the chamber. The anterior end of the septal neck gives way to the organic membrane of the siphuncle. Inside and projecting slightly rearward there is a cuff, which gives way at the rear to the organic membrane of the siphuncle.

The ventral spines are formed by inflections of all layers of the shell wall; in contrast to Kosmoceras, the dorsal wall is covered in spines following their contour. The septa are inserted on the lateral sides of the spines.

Sigaloceras is similar to the genus Kosmoceras in many internal structural characters. The shape and size of the protoconch are approximately the same, the shell diameter of the ammonitella is approximately 0.85, the nepionic line is located at a distance of approximately 315° from the proseptum, there are nine to eleven septa in the first four whorls, less frequently 12. The position of the siphuncle and the structure of the septal necks vary uniformly in the course of ontogeny. The nature of the damage to the shell wall and the mode of its healing are monotypic. The fixator is slightly longer in the genus Sigaloceras than in Kosmoceras.

* * *

Features in common, which are probably typical of many ammonoid groups, may be found in shell structure between the members of the families investigated. They include: 1) the prismatic microstructure of the protoconch wall and the first whorl as far as the nepionic line, the structure of the nepionic ridge developed from the nacreous layer, the structure of the shell wall after the nepionic line (initially two-layered, subsequently three-layered with a well developed nacreous layer); 2) alteration in the position of the siphuncle in ontogeny (from central in the first whorl to ventromarginal at the end of the second - beginning of the third) and a reduction in its relative diameter; 3) short prochoanitic septal necks accompanied by small cuffs and annular deposits.

Differences: 1) the greater and lesser diameters of the protoconch are slightly greater in the Cardoceratinae than in the Kosmoceratinae (D^1 is 0.48 to 0.55 in the former, 0.39 to 0.49 in the latter; D^2 is 0.38 to 0.40 in the former, 0.34 to 0.39 in the latter), 2) the shell diameter of the ammonitella is 0.83 to 0.87 in the Cardoceratinae, 0.76 to 0.85 in the Kosmoceratinae; 3) the angle of the nepionic line is 260 to 280° in the former, 310 to 315° in the latter; 4) there are considerably more septa in the first four whorls in the Cardoceratinae (16 to 22) than in the Kosmoceratinae (nine to eleven), and the curves depicting variation in the distance between septa are correspondingly different.

It does not seem possible at the present time to evaluate the rank of the differences enumerated or to answer questions concerning the generic links between the Cardioceratidae and the Kosmoceratidae. Additional research on the families under consideration, including their ancestors and descendants, is needed for this purpose.

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